

OCCURRENCE OF THE INVASIVE SPECIES *POTAMOPYRGUS ANTIPODARUM* (PROSOBRANCHIA: HYDROBIIDAE) IN MINING SUBSIDENCE RESERVOIRS IN POLAND IN RELATION TO ENVIRONMENTAL FACTORS

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ABSTRACT

The New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843), is recognized as a successful invader of aquatic environments in Australia, Europe, Japan, North America and western Asia. To date, a long-term survey on the occurrence of *P. antipodarum* (including its initial dispersal, establishment and integration) both in mining subsidence reservoirs and an adjacent river in Poland has not been carried out. The objectives of this survey were to analyze the environmental factors that influence the occurrence of *P. antipodarum* in relation to mollusc communities in mining subsidence reservoirs affected by coal mine output in terms of initial dispersal and the establishment of self-sustaining populations in the new habitat, to analyze annual variations in the densities and shell height of *P. antipodarum* in relation to the different types of substratum, and to determine the number of embryos in the brood pouch per female at the integration stage (phase). During the years 1993–2008, seven mining subsidence reservoirs that have different water sources and a part of the Mleczna River were investigated.

From 1997 to the present, *P. antipodarum* has been eudominant in mollusc communities both in coal mining subsidence reservoirs, which receive water from the mine dewatering system and in the river. Based on a redundancy analysis (RDA), the conductivity of water and the concentration of nitrates were the parameters most associated with the distribution of mollusc species, including *P. antipodarum*. The relation between the species and these environmental variables was statistically significant.

These results do not suggest that the integration of *P. antipodarum* has negatively influenced the occurrence of other mollusc species either in the mining subsidence reservoirs or in the Mleczna River, probably due to smaller densities compared with a survey of the western United States, where *P. antipodarum* has a strong influence on aquatic ecosystems and restricts the occurrence of native macroinvertebrates. *Potamopyrgus antipodarum* has established itself in these mining subsidence reservoirs and is integrated into the local biota without any major negative effects (e.g., extirpations) on the communities being invaded.

Key words: *Potamopyrgus antipodarum*, alien species, RDA, environmental factors, shell height, embryos, mining subsidence reservoirs.

INTRODUCTION

One of the factors that influences the species balance in native aquatic fauna is the arrival of new species from other geographical areas. A new species may become integrated into the local biota without extinctions of native organisms or may have a range of effects on the extirpation of native species. The general process of an invasion can be divided into three basic stages: arrival (initial dispersal), establishment of self-sustaining populations

within the new habitat, and integration (Moyle & Light, 1996; Puth & Post, 2005) or to be more detailed, into five stages: from 0 (a donor region) to V (widespread and dominant) (Colautti & MacIsaac, 2004).

The New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843), is recognized as a successful invader of aquatic environments in Australia, Europe, Japan, North America (Ponder, 1988; Mitsuaki & Ryoji, 2004; Richards & Shinn, 2004) and western Asia (Naser & Son, 2009).

In Europe, *P. antipodarum* was recorded for the first time (initial dispersal) in England at Grays, Essex before 1852 (Kerney, 1999). It was probably introduced there by way of drinking water supplies on ships and then liberated into such estuarine areas as the River Thames during the washing or filling up of water barrels or tanks (i.e., transported out of its native range via long-distance transport vectors and then released within a new locality).

Potamopyrgus antipodarum has successfully colonized freshwater and brackish habitats in almost all of Europe: Great Britain (Fish & Fish, 1989; Kerney, 1999), the Iberian Peninsula (Sousa et al., 2007a; Múrria et al., 2008), France, Finland (Carlsson, 2000; Leppäkoski & Olenin, 2000), Sweden, Russia, Belarus (Karatayev et al., 2008), Lithuania, Latvia, the Ukraine (Con, 2006), Slovakia (Šteffek, 2000), the Czech Republic (Beran, 2002), Austria (Patzner, 1996), Switzerland (Baur & Ringeis, 2002), Hungary (Héra, 2005) and Greece (Radea et al., 2008).

In Poland, *P. antipodarum* was recorded for the first time in inland waters in its initial dispersal stage in 1933. At present, this invasive species occurs in brackish and freshwater habitats in many parts of Poland (Jackiewicz, 1973; Strzelec, 1993; Brzeziński & Kołodziejczyk, 2001). In Upper Silesia, southern Poland, *P. antipodarum* was recorded for the first time in a sand pit pond in 1986 (Strzelec & Krodzewska, 1994) (stage II: introduction). Currently, *P. antipodarum* has inhabited most aquatic environments in Upper Silesia: rivers, streams and anthropogenic reservoirs (Strzelec, 1999a; Michalik-Kucharz et al., 2000; Lewin & Smoliński, 2006); this is the third (III) stage establishment.

Colonization and dispersal of *P. antipodarum* is enhanced by parthenogenesis (Wallace, 1979, 1992) and is euryhaline. These factors could be major contributors to the rapid rate of the New Zealand mud snail's spread (establishment of self-sustaining populations within the new habitat) throughout Europe. Salinity is an important range limitation factor for most aquatic species compared to other ecological factors, such as food supply, competition, and predators. *Potamopyrgus antipodarum* is able to tolerate salinity of up to 28‰ (Costil et al., 2001) or even up to 30‰ (Paavola et al., 2005). *Potamopyrgus antipodarum* may be transferred by many local and long-distance vectors, such as birds, fish, insects, lymnaeid snails (when ingested by them, they can go through the

digestive system and remain alive) (Piechocki, 1999; Piechocki & Kaleta, 2001; Vinson, 2004; Bersine et al., 2008), fish stocking and angling (Loo et al., 2007); boats and ships (attached to their hulls), through the ballast water of commercial ships, within freshwater tanks and water pipes (Alonso & Castro-Díez, 2008).

Potamopyrgus antipodarum occurs more frequently at aquatic sites with multiple land uses in a catchment area compared to sites with low-impact human activities (Schreiber et al., 2003). A wide tolerance range to physical and chemical factors, the ability for active and passive dispersal, ovoviviparity, parthenogenesis and a high reproduction rate may explain the spread and integration success of *P. antipodarum*. For example, in the USA, *P. antipodarum* can produce up to six generations per year and reproduction appears to be the highest during the summer months (Vinson, 2004).

Some data have indicated that *P. antipodarum* influences the impoverishment of native fauna in reservoirs in industrial areas (Strzelec, 2005). At extremely high densities, *P. antipodarum* may compete for food and the space occupied by native non-molluscan fauna (Strayer, 1999) or native snails (Department of the Interior, U.S. Geological Survey, 2002).

Upper Silesia, southern Poland, is the most urbanized and industrialized region with a natural environment that has been transformed over two hundred years, deteriorated on a large scale and polluted mainly by hard coal mining or the metallurgical industry. This area constitutes one of the biggest coal basins in the world. It has been mined since the eighteenth century. Upper Silesia has no natural water bodies; only reservoirs of an anthropogenic origin, including mining subsidence reservoirs are common. Most of these as well watercourses are characterized by high levels of chlorides, sulphates, TDS, biogenic elements, conductivity (of even up to 20,000 µS/cm) or heavy metals both in the water and bottom sediments (Rzetała, 2008). Anthropogenic reservoirs, which are not so degraded, have provided refuges for many species of fauna and flora as well as rare and vulnerable mollusc species. Thus, they constitute important lentic habitats in Upper Silesia.

To date, a long-term survey on the occurrence of *P. antipodarum* (including its initial dispersal, establishment and integration) both in mining subsidence reservoirs and the river has not been carried out.

The objectives of the survey were to (1) analyze the environmental factors which influence

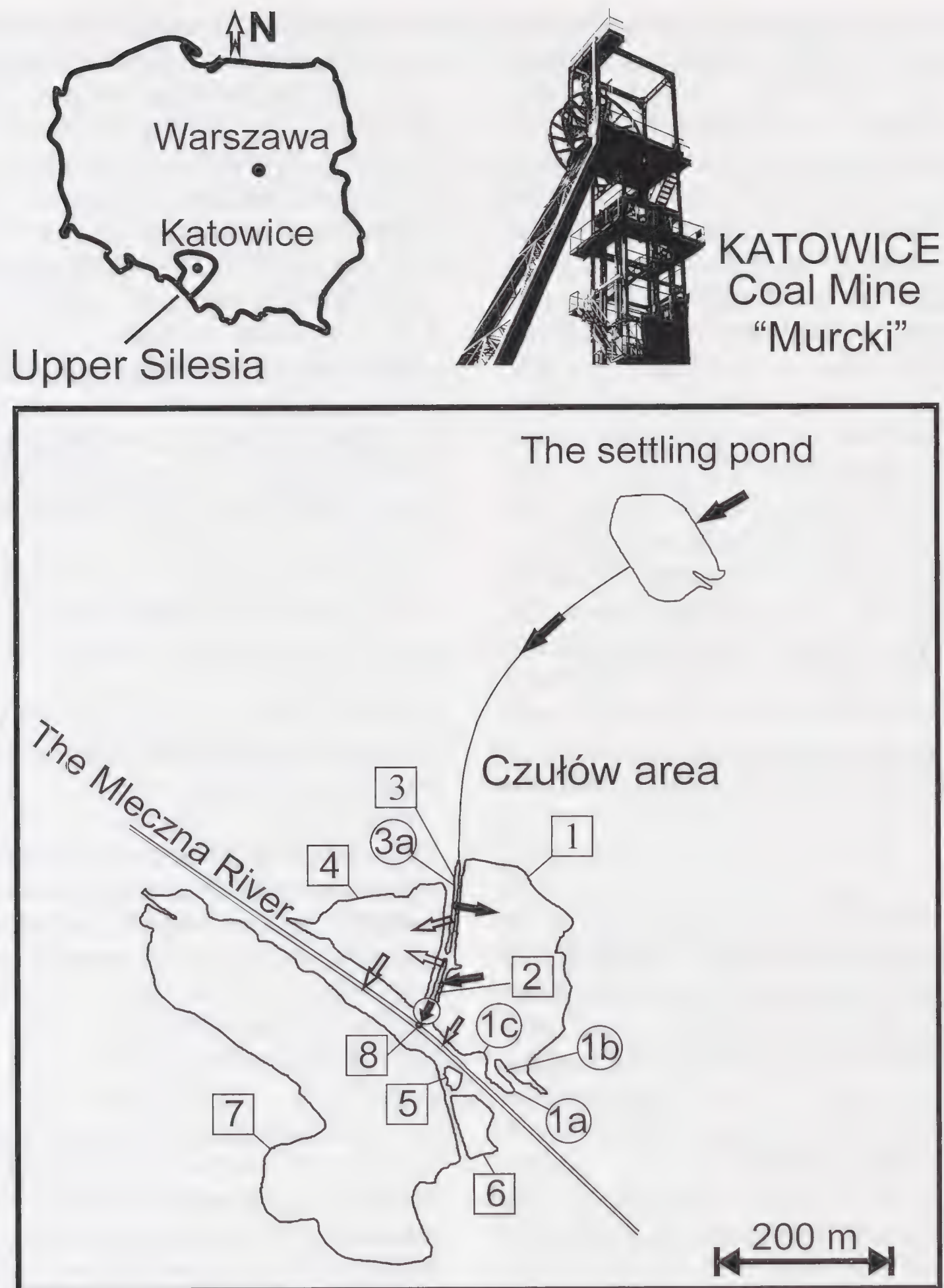


FIG. 1. Location of the study area. Sampling sites (biometrical analysis): 1, 2, 3, 4 = mining subsidence reservoirs with flowing water; 5, 6, 7 = mining subsidence reservoirs with non-flowing water; 1a = submerged leaves of *Glyceria maxima*; 1b = submerged leaves of *Typha latifolia*; 1c = muddy-stony bottom; 3a = muddy-sandy bottom; white arrow = water flow; black arrow = main water stream of the mining dewatering system.

the occurrence of the invasive species *P. antipodarum* in relation to mollusc communities in mining subsidence reservoirs affected by coal mine output in terms of initial dispersal and (2) the establishment of self-sustaining populations within the new habitat, (3) to analyze annual variations in densities and shell height of *P. antipodarum* in relation to the different types of substratum and (4) to determine the number of embryos in the brood pouch per female at the integration stage (phase).

MATERIALS AND METHODS

Study Area

The study was carried out from 1993–2008 in Czułów near Katowice, Upper Silesia, southern Poland. Seven mining subsidence reservoirs with different water sources were investigated. The part of the Mleczna River, which is connected with the mining subsidence reservoirs, was also investigated. The reservoirs were

developed from the operation of the "Murcki" coal mine in the 1970s. The mining subsidence reservoirs 1, 2, 3 and 4 (Fig. 1) are supplied with flowing water from surface waters and also with waters from the mine dewatering system. Mining water flows into reservoir 3 and then through reservoirs 1, 2, 4 and on into the Mleczna River. Mining subsidence reservoirs 5, 6, and 7 are reservoirs with non-flowing water. The surface areas of the reservoir amounts to: 100 (No. 5), 150 (No. 2), 240 (No. 3), 2,400 (No. 6) 3,200 (No. 4), 5,000 (No. 1) and 25,000 (No. 7) m², respectively. The average depth of the reservoirs ranges from 0.5 to 2.0 m. The reservoirs have now been reclaimed and the banks are partially concrete-lined and stabilized with waste rock and slag. The reservoirs, which are stocked with fish, are used by anglers and hunters. The macrophytes have been partially removed and the reservoirs' output has been regulated as part of the reservoir management process. This area provides a refuge for wild-fowl, birds of prey, amphibians and reptiles.

Methods

Samples of Molluscs and Water: Molluscs were sampled once each year from 1993–2008 using a 25 x 25 cm quadrat frame placed randomly in 16 locations (sampling area: 1 m²) within each of the reservoir beds and the river. Bottom sediments up to 5 cm, macrophytes and surface water were included within each sample. The collected material was sealed in plastic bags and plastic containers. The samples were then filtered using a 0.5 mm mesh sieve, sorted, and then the molluscs were preserved in 75% ethanol. The species of molluscs were identified according to Glöer & Meier-Brook (1998) and Glöer (2002). Mollusc density was estimated as the number of individuals per square meter. Water samples were collected from each sample site immediately prior to sampling and analyzed for the physical and chemical parameters of the water, that is, conductivity, pH, dissolved oxygen, nitrates, phosphates, total hardness, iron, chlorides and alkalinity. The total hardness was considered within following ranges: soft water from 90 to 180 mg CaCO₃/l, medium hard water above 180 to 270 mg CaCO₃/l, significantly hard above 270 to 360 mg CaCO₃/l, and hard water up to 450 mg CaCO₃/l (Hermanowicz et al., 1999). The significance of differences in the physical and chemical parameters among reservoirs with flowing water, non-flowing water and the river

was calculated by means of the Kruskal-Wallis one-way ANOVA test using the Statistica program version 8.0 (the value of parameters did not reveal a normal distribution and this justified the use of a non-parametric test).

For the biometrical analysis (e.g., the shell height measurement), every month, from June 2006 to June 2007, *P. antipodarum* were collected from a range of substrata in reservoir 1 (three sampling sites): sampling site (1a) submerged leaves of *Glyceria maxima* (Hartm.) Holmb., sampling site (1b) submerged leaves of *Typha latifolia* L., sampling site (1c) muddy-stony bottom and in reservoir 3 (one sampling site): sampling site (3a) muddy-sandy bottom, in order to sample the most microhabitats (Fig.1). Shell height was measured for 100 specimens of *P. antipodarum* randomly chosen from each of the sampling sites in each of the months. Each month, the number of embryos in the brood pouch was assessed for 30 specimens for which the shell height was larger than 3.5 mm.

Zoocenological Study: A zoocenological study of the mollusc communities was carried out to evaluate the dominance pattern of *P. antipodarum* in relation to other mollusc species:

(1) Dominance (D%)

$$D = n_a / n \times 100$$

where

n_a - the number of individuals of species a,

n - the total number of individuals in a sample.

The value of the dominance index D was divided into five classes according to Górny & Grüm (1981): eudominants > 10.0% of sample, dominants 5.1–10.0% of sample, subdominants 2.1–5.0% of sample, recedents 1.0–2.1% of sample, and subrecedents < 1.0% of sample.

(2) The Shannon-Wiener index (Cao et al., 1996; Mouillot & Lepretre, 1999)

$$H' = - \sum (P_i) (\log_2 P_i)$$

where

$P_i = N_i / N$ - the proportion of individuals belonging to species i.

The values of H' were calculated using the Multi-Variate Statistical Package version 3.1.

Redundancy Analysis (RDA): Canonical ordination analyses for relating the species composition of mollusc communities to their environment were carried out using CANOCO for Windows version 4.5 (Ter Braak & Šmilauer, 2002). The appropriate type of analysis (re-

TABLE 1. Physical and chemical parameters of water and their values (ranges) of the Mleczna River and mining subsidence reservoirs with flowing water compared to mining subsidence reservoirs with non-flowing water in the years 1993–2008.

Parameter	The Mleczna River (main overflow) No. 8	Reservoirs 1, 2, 3, 4 (flowing water)	Reservoirs 5, 6, 7 (non-flowing water)
Conductivity (μS/cm)	1800–3240	710–3020	290–1500
pH	7.0–7.9	7.0–8.3	7.1–8.4
Dissolved oxygen (mg O ₂ /l)	2.4–10.8	3.1–11.0	3.5–11.3
Nitrates (mg NO ₃ /l)	0.3–208.2	1.0–194.9	1.3–51.4
Phosphates (mg PO ₄ /l)	0.41–4.02	0.21–2.74	0.04–2.10
Total hardness (mg CaCO ₃ /l)	270–450	218–357	35–246
Iron (mg Fe/l)	0.19–1.50	0.09–1.50	0.01–1.39
Chlorides (mg Cl/l)	432–450	67–665	25–300
Alkalinity (mg CaCO ₃ /l)	260–365	140–390	85–225

dundancy analysis) was chosen to analyze the species data by DCA (Detrended Correspondence Analysis) and the length of the gradient. Preliminary DCA on the species data revealed that the gradient length was less than 3 SD (three standard deviation) indicating that the species exhibited linear responses to underlying environmental variation which justified the use of linear multivariate methods. Therefore, a linear direct ordination technique RDA with a forward selection was used to reduce the large set of environmental variables. The statistical significance of the relationship between the mollusc species and the physical and chemical parameters of water was evaluated using the Monte Carlo permutation test (499 permutations) (Ter Braak & Šmilauer, 2002).

Densities: Variations in densities of *P. antipodarum* at sampling sites in the mining subsidence reservoirs which receive water from a mine dewatering system and in the Mleczna River were recorded from June 2006 to June 2007.

The significance of differences in the density of *P. antipodarum* in the sampling sites were calculated by means of the Kruskal-Wallis one-way ANOVA test using the Statistica program version 8.0.

Shell Height and Number of Embryos: The significance of the differences in the shell height of *P. antipodarum* from particular sampling sites (four sampling sites) was calculated by means of the Kruskal-Wallis one-way ANOVA test. The relationship between the shell height

of *P. antipodarum* and the number of embryos in the brood pouch per female was calculated by means of the non-parametric test of the Spearman Rank Correlation Coefficient r_s . The data of the shell height and the number of embryos in the brood pouch of *P. antipodarum* did not reveal a normal distribution; therefore, non-parametric tests were applied. The statistical analysis was performed using the Statistica program version 8.0.

RESULTS

Water Physical and Chemical Parameters

The water from both the mining subsidence reservoirs with flowing water that receive water from a mine dewatering system and in the Mleczna River was high in conductivity, phosphates, chlorides and very high in nitrates compared to the reservoirs with non-flowing water (Table 1). The waters are soft and medium hard in reservoirs with non-flowing water (nos. 5, 6, 7), medium hard and significantly hard in reservoirs with flowing water and significantly hard or hard in the Mleczna River. The Kruskal-Wallis one-way ANOVA test revealed statistically significant differences in conductivity $H(2, N = 36) = 21.35$, $p = 0.0001$; alkalinity ($H = 21.04$, $p = 0.0001$); chlorides ($H = 20.04$, $p = 0.001$); total hardness ($H = 22.11$, $p = 0.0001$); iron ($H = 10.14$, $p = 0.01$) between the reservoirs with non-flowing and flowing water and the river. Nitrates ($H = 14.86$, $p = 0.001$) and phosphates ($H = 12.42$,

TABLE 2. Values of the dominance (D%) and the Shannon-Wiener (H') indices of the mollusc communities in mining subsidence reservoirs with flowing water.

Species	Years of survey												
	1993	1995	1996	1997	2000	2001	2002	2003	2004	2005	2006	2007	2008
<i>Viviparus contectus</i> (Millet, 1813)			6.6	0.4	0.8	2.9	2.4	3.4	5.5	0.6	0.8	0.3	0.4
<i>Bithynia tentaculata</i> (Linnaeus, 1758)					7.2	2.2	3.1	3.5	9.2	3.9	3.3	7.0	0.7
<i>Potamopyrgus antipodarum</i> (J. E. Gray, 1843)				83.0	51.8	66.4	38.4	40.5	43.5	81.4	85.1	89.9	96.5
<i>Acroloxus lacustris</i> (Linnaeus, 1758)	36.4	31.6	1.9	0.1	7.6	0.7		1.5	1.6	0.3	2.0	0.3	0.2
<i>Stagnicola palustris</i> (O. F. Müller, 1774)			3.8	0.4									
<i>Stagnicola corvus</i> (Gmelin, 1791)			1.9	0.5									
<i>Radix auricularia</i> (Linnaeus, 1758)					4.0		1.8	0.4	1.0	0.1	0.4	0.1	0.1
<i>Radix balthica</i> (Linnaeus, 1758)	24.5	24.7	22.6	1.6	4.8	1.9	4.3	3.2	12.6	1.0	0.6	0.2	0.2
<i>Lymnaea stagnalis</i> (Linnaeus, 1758)	13.2	14.6	1.9	0.9	1.6	3.6	7.9	16.2	4.4	0.5	0.7	0.3	0.4
<i>Physella acuta</i> (Draparnaud, 1805)			9.4	2.4			1.8	0.3		0.5	0.8	0.3	0.3
<i>Aplexa hypnorum</i> (Linnaeus, 1758)									0.4	0.2	0.3	0.1	0.1
<i>Planorbarius corneus</i> (Linnaeus, 1758)	6.6	3.8	16.0	0.7	9.7	6.0	6.7	13.2	3.4	0.4	1.4	0.4	0.2
<i>Ferrissia wautieri</i> (Mirolli, 1960)							1.8	0.3					
<i>Anisus spirorbis</i> (Linnaeus, 1758)			3.8	2.3		0.5							
<i>Bathyomphalus contortus</i> (Linnaeus, 1758)				0.1					0.3		0.2	0.1	0.1
<i>Gyraulus albus</i> (O. F. Müller, 1774)	6.0	7.0	3.8	1.2	8.8	2.2	6.7	3.2	2.4	0.3	0.4	0.2	0.1
<i>Gyraulus crista</i> (Linnaeus, 1758)	1.3	6.3		0.2	1.6		3.7	1.8	7.8	4.2	0.5	0.2	0.1
<i>Hippeutis complanatus</i> (Linnaeus, 1758)			15.1	5.3	2.0	4.1	6.7	2.4	2.3	2.0	0.9	0.1	0.2
<i>Segmentina nitida</i> (O. F. Müller, 1774)	12.0	12.0	13.2	1.0		3.4	9.2	3.7	4.1	3.3	0.6	0.1	0.2
<i>Anodonta anatina</i> (Linnaeus, 1758)									0.6	0.2	0.3	0.1	0.04
<i>Sphaerium corneum</i> (Linnaeus, 1758)											0.8	0.2	0.1
<i>Musculium lacustre</i> (O. F. Müller, 1774)						4.8	3.1	2.1	0.4	0.2	0.5	0.1	0.1

(continues)

(continued)

Species	Years of survey												
	1993	1995	1996	1997	2000	2001	2002	2003	2004	2005	2006	2007	2008
<i>Pisidium casertanum</i> (Poli, 1791)						1.2	2.4	4.3	0.7	0.9	0.6	0.2	0.1
Σ of species	7	7	12	15	11	13	15	16	17	17	19	19	19
Σ of specimens	151	158	106	1,726	249	414	164	677	708	3,188	2,465	7,078	11,671
Value of the H'	2.36	2.49	3.22	1.18	2.44	2.03	3.22	2.89	2.88	1.80	1.16	0.69	0.41

$p = 0.002$) varied between the reservoirs with non-flowing water and the river.

Occurrence in Relation to Mollusc Communities and Values of Shannon-Wiener Index

Between 1993–2008, 23 species of molluscs were observed in the reservoirs with flowing water (Table 2), whereas only ten species were found in the Mleczna River (Table 3).

In 1997, *P. antipodarum* started to occur in the reservoirs with flowing water and in the Mleczna River, and it has become eudominant in the mollusc communities (Tables 2, 3). *Potamopyrgus antipodarum* is absent from the mining subsidence reservoirs with non-flowing waters.

The number of mollusc species increased from 1993–1996, reaching 15 in 1997 and collapsed to 11 in 2000. In the next few years, the number of species increased once again reaching 19 in 2006 (Table 2). Bivalve species: *Anodonta anatina*, *Sphaerium corneum*, *Musculium lacustre* and *Pisidium casertanum* were subprecedents in the mollusc communities from 2004 to the present in the mining subsidence reservoirs. In 1997–2008, the number of mollusc species increased from 3 to 10 in the Mleczna River (Table 3).

The Shannon-Wiener index values calculated for mollusc communities ranged from 0.41 to 3.22 in the reservoirs with flowing water and from 0.97 to 3.11 in the Mleczna River (Tables 2, 3).

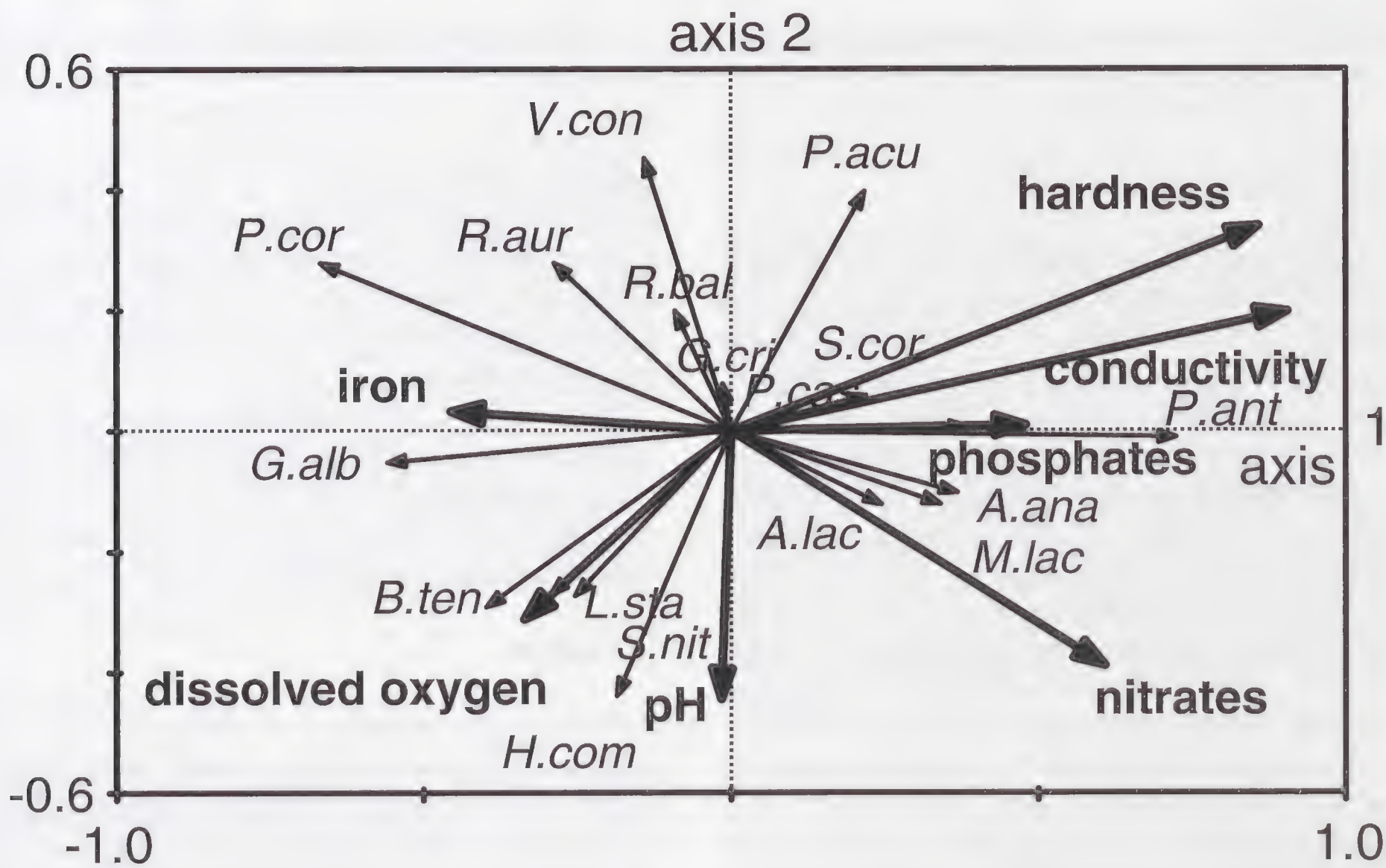


FIG. 2. Ordination diagram (biplot) based on a redundancy analysis (RDA) of the mollusca data including *P. antipodarum* and environmental variables. The long arrows representing some environmental variables emphasize their great impact on the community structure of Mollusca.

TABLE 3. Values of the dominance (D%) and the Shannon-Wiener (H') indices of the mollusc communities (Mleczna River).

Species	Years of survey												
	1993	1995	1996	1997	2000	2001	2002	2003	2004	2005	2006	2007	2008
<i>Viviparus contectus</i> (Millet, 1813)													3.5
<i>Bithynia tentaculata</i> (Linnaeus, 1758)						13.9	21.9	23.1	16.1	11.3	7.3	4.8	4.2
<i>Potamopyrgus antipodarum</i> (J. E. Gray, 1843)				47.2	39.3	41.7	25.0	26.92	29.0	22.6	13.8	48.7	11.9
<i>Radix auricularia</i> (Linnaeus, 1758)						8.3	15.6	15.4	19.4	13.2	11.0	5.9	2.8
<i>Radix balthica</i> (Linnaeus, 1758)	60	55.6	56.2	27.8	32.1	19.4	15.6	15.4	16.1	7.6	3.7	2.7	6.3
<i>Lymnaea stagnalis</i> (Linnaeus, 1758)	40	44.4	43.8	25.0	28.6	16.7	21.91	19.2	12.9	13.2	12.8	7.5	12.6
<i>Physella acuta</i> (Draparnaud, 1805)										20.8	44.0	24.6	50.3
<i>Gyraulus albus</i> (O. F. Müller, 1774)										3.8	2.8	2.7	4.9
<i>Sphaerium corneum</i> (Linnaeus, 1758)										3.8	2.8	1.6	2.1
<i>Musculium lacustre</i> (O. F. Müller, 1774)									6.4	3.8	1.8	1.6	1.4
Σ species	2	2	2	3	3	5	5	5	6	9	9	9	10
Σ specimens	15	18	16	36	28	36	32	26	31	53	109	187	143
Value of the H'	0.97	0.99	0.99	1.52	1.60	2.11	2.30	2.29	2.46	3.11	2.49	1.97	2.41

Redundancy Analysis (RDA)

Species and environmental variables based on the first two axes explain 38.95% of the variance in the species data and 89.05% of the variance in the fitted species data. Based on the redundancy analysis (RDA), the conductivity and the concentration of nitrates were the parameters most associated (statistically significant according to the forward selection results) with the distribution of mollusc species, including *P. antipodarum* (Fig. 2). The most important parameter contributing to RDA axis 1 was conductivity. Two different patterns of mollusc distribution were found: (1) *Potamopyrgus antipodarum* was the species situated close to the arrow indicating conductivity and *Gyraulus albus* was the species situated on the opposite side, (2) *Acroloxus lacustris* and the bivalves *Anodonta anatina* and *Musculium lacustre* were the groups of species situated close to the arrow indicating nitrates and *Plan-*

orbarius corneus was the species situated on the opposite side. Angles between the arrows of species and environmental variables in an ordination diagram from linear methods show a positive (acute angle) or a negative (straight angle) correlation.

The relation between the species and the environmental variables was statistically significant (test of significance of first canonical axis: $p = 0.016$, $F = 10.904$, test of significance of all canonical axes: $p = 0.012$, $F = 2.328$).

Densities

The mean density of *P. antipodarum* in the mining subsidence reservoirs with flowing water between June 2006 to June 2007 was $1,875.4 \pm 1,670.01$ individuals/m² ($\pm$ the standard deviation). The densities of *P. antipodarum* increased to 6,010 individuals/m² (Fig. 3) between June 2006 to August 2006. The densities showed a decreasing tendency from August

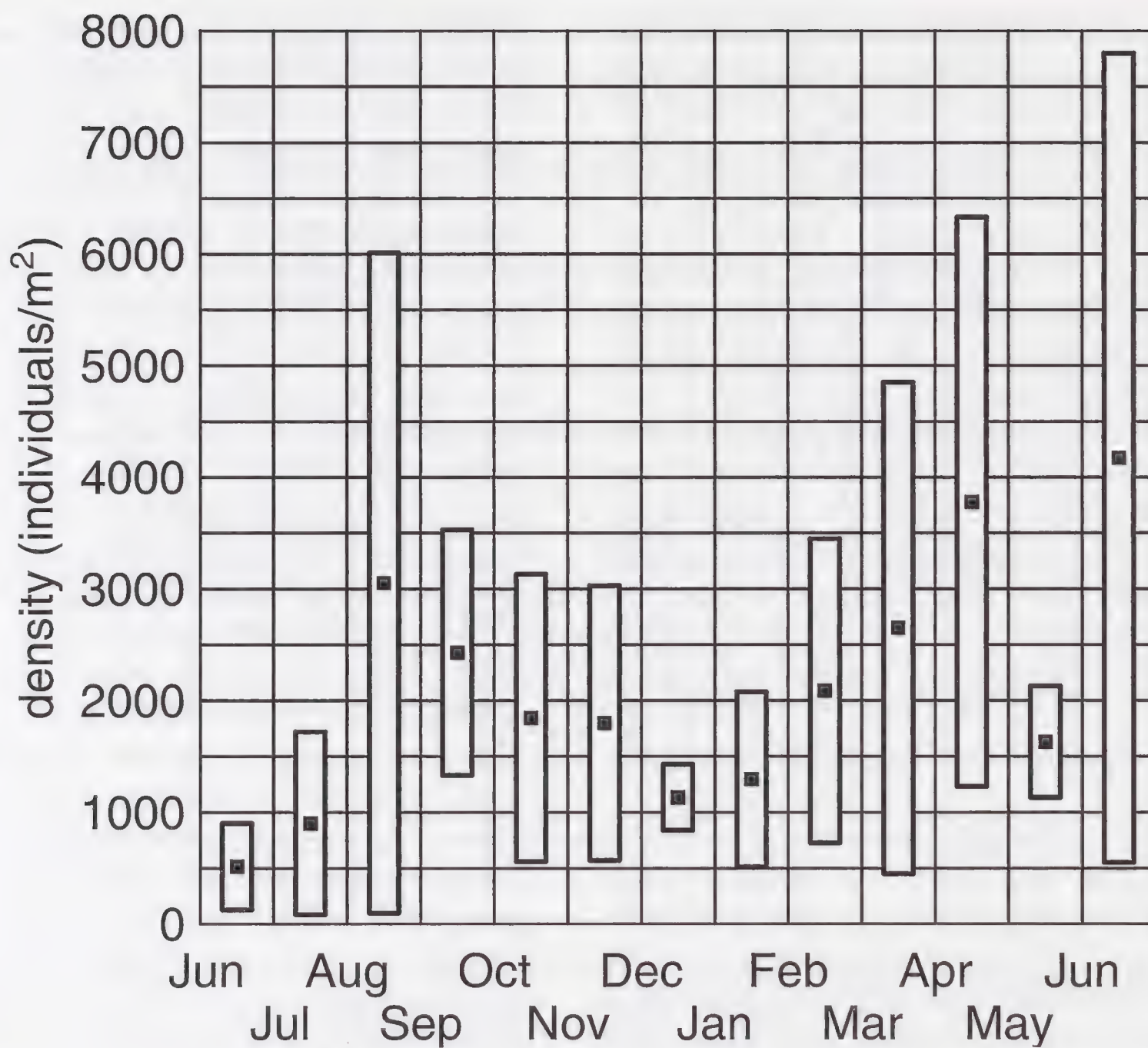


FIG. 3. Densities (mean and ranges) of *P. antipodarum* in the mining subsidence reservoirs with flowing water (individuals/m²), June 2006–June 2007; ■ = mean; □ = $\pm$ SD.

2006 to December 2006 (to 560 individuals/m² in December). From January 2007 the densities gradually increased again (Fig. 3). The lowest densities of 85 individuals/m² were recorded at sampling site 1c (July 2006), while the highest densities of 7,800 individuals/m² were recorded at sampling site 1b (June 2007). The Kruskal-Wallis one-way ANOVA test revealed a lack of statistically significant differences in *P. antipodarum* densities both at the sampling sites in particular months of the survey ($H(51, N = 52) = 51.0, p = 0.47$) and at sampling sites 1a, 1b, 1c, 3a in a particular month of the survey ($H(12, N = 13) = 12.0, p = 0.45$). The densities were low in the Mleczna River and ranged from 3 to 86 individuals/m².

Shell Height

The mean shell height of *P. antipodarum* varied depending on the sampling sites. The highest mean shell height of 4.42 ± 0.38 mm was recorded in October 2006 (sampling site 1b, submerged parts of leaves of *Typha latifolia*), while the lowest mean shell height of

3.31 ± 0.87 mm was recorded on submerged leaves of *Glyceria maxima* (site 1a) in January 2007. The maximum shell height was 6.96 mm (September, sampling site 1b). At sampling sites 1a and 1c the highest mean shell height was recorded in April 2007 and the lowest mean shell height in January. At sampling site 3a the highest mean shell height was recorded in June 2006. To conclude, low mean shell height was recorded twice in the year: in winter in January (sampling sites 1a and 1c) or February (sampling sites 1b and 3a) and in summer in July or August (sampling sites 1a, 1b and 1c). The Kruskal-Wallis one-way ANOVA test revealed statistically significant differences in the shell height of *P. antipodarum* among the sampling sites in each of the months of the survey ($p = 0.001$).

Number of Embryos in Brood Pouch

From June 2006 to June 2007 the mean number of embryos per female was 11.83 ± 10.23 ($\pm$ the standard deviation). The highest mean number per female was recorded in April 2007

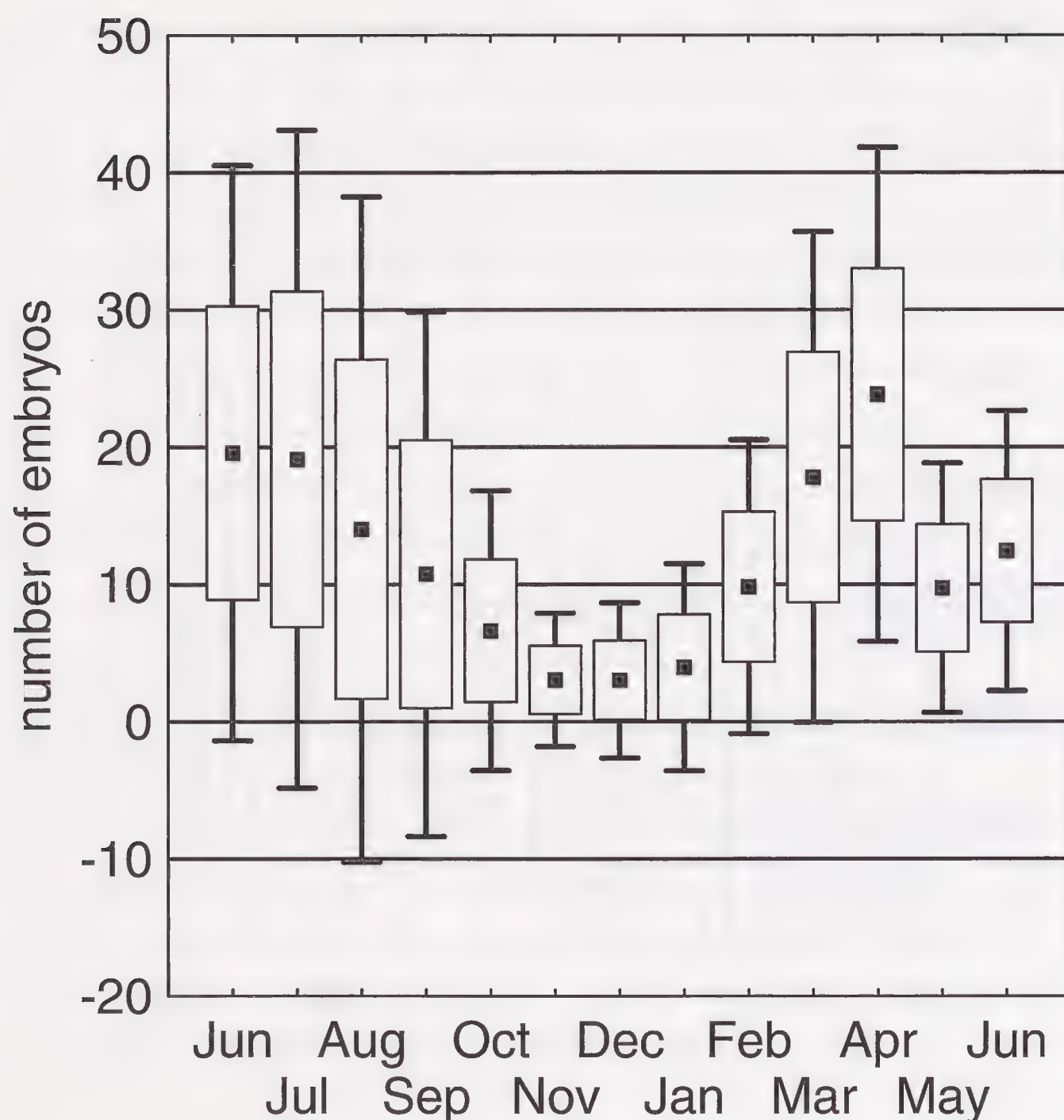


FIG. 4. The monthly mean number of embryos with SD in the brood pouch per female of *P. antipodarum*, June 2006–June 2007; ■ = mean; □ = $\pm$ SD; I $\pm$ 1.96 SD.

(23.83 ± 9.19); the lowest in December 2006 (3.02 ± 2.89) (Fig. 4). From December 2006 to April 2007, the number of embryos increased gradually, and subsequently decreased in May 2007. The maximum number of embryos amounted to 59 (April 2007). The embryos were recorded in the brood pouch in females with a shell height over 3.0 mm. Analysis of the Spearman Rank Correlation coefficient r_s showed a statistically significant correlation between shell height and the number of embryos per female in each of the months of the survey ($N = 120$, $p < 0.05$).

DISCUSSION

Invasion Stages within Mining Subsidence Reservoirs and the River

This long-term survey of the occurrence of *P. antipodarum* both in mining subsidence reservoirs and the Mleczna River in Upper Silesia disclosed novel findings about the invasion

process, from its initial dispersal to establishment and integration. According to Colautti & MacIsaac (2004) and Colautti et al. (2006), the invasion process is broken into stages from stage 0 (donor region) to stage V (widespread and dominant), with sequential filters that act to preclude transition between particular stages. The results of this study showed that *P. antipodarum* was not collected in 1996 and that within one year, a rapid increase in its density was observed (transformation from stage III: localized and numerically rare to stage IVb: localized but dominant). Probably, during the initial dispersal of *P. antipodarum* within the mining subsidence reservoirs or river, the population was too small to be detected (stage III). This survey confirmed a similar pattern of the occurrence of *P. antipodarum* at its initial dispersal and establishment stage in the water environments of Upper Silesia obtained by Strzelec & Krodziewska (1994).

Parthenogenesis and euryhalinity may explain the ability of *P. antipodarum* to increase in abundance and then lead to its successful

establishment (which could be expressed as its invasiveness characteristics or effectiveness of propagule pressure) within these reservoirs from 1996 to today. Considering the framework of Colautti & MacIsaac (2004), the population of *P. antipodarum* seems to be localized but dominant (stage IVb) within mining subsidence reservoirs with flowing water on a local scale. Reservoirs with non-flowing water compared to reservoirs with flowing water may be relatively invulnerable to invasions of *P. antipodarum*. It is possible that the movement of water both within subsidence reservoirs and in the Mleczna River is one of the dispersal vectors that enables *P. antipodarum* to spread. Other local dispersal vectors may also be important within mining subsidence reservoirs and the Mleczna River in addition to water movement, for example, fish and wildfowl, including migratory birds. These reservoirs are stocked with fish (Lewin & Smoliński, 2006), and many species of birds have been observed there. *Potamopyrgus antipodarum* may be ingested by them and may go through the digestive system unharmed to be excreted elsewhere or snails may be transported in mud on the feet or feathers of migratory birds or fishermen.

Invasive species must pass through at least three of the invasion stages before they are able to inflict ecological or economic harm, that is, transport, introduction, establishment, spread and impact (Lockwood et al., 2007). This survey did not show that *P. antipodarum* has had a negative influence on native mollusc species and at such a density is probably not able to inflict ecological or economic harm. However, a survey on the influence of *P. antipodarum* on other macroinvertebrates in these reservoirs was not carried out.

Occurrence in Relation to Mollusc Communities

These surveys found a few mollusc species that are rare for the Silesian Upland, southern Poland, that is, *Viviparus contectus*, *Physella acuta*, *Hippeutis complanatus*, and *Anodonta anatina*. Some of these are considered to be uncharacteristic species for this region, including *Bithynia tentaculata*, *Radix auricularia*, *Segmentina nitida*, *Musculium lacustre* and *Pisidium casertanum*. According to Strzelec (1993), *P. antipodarum* was a rare species in this region. This survey found the occurrence of *Bithynia tentaculata*, *Radix auricularia*, *Stagnicola palustris*, *Hippeutis complanatus* and *Ferrissia wautieri* for the first time in the mining subsidence reservoirs of Upper Silesia.

In 2000, 2004 and 2007 *Bithynia tentaculata* was dominant in the mollusc communities. *Ferrissia wautieri* was recorded in reservoirs with flowing water in the years 2002–2003. This species was first found in France in 1944 (Mirolli, 1960; Hubendick, 1972). *Ferrissia wautieri* is now considered to be a synonym of the North American *Ferrissia fragilis* (Tryon, 1863) (Walther et al., 2006; Walther, 2007). In 1997–2008, *P. antipodarum* was eudominant in the mollusc communities both in reservoirs with flowing water and in the Mleczna River. This result is consistent with the survey done by Strzelec & Krodzińska (1994) or Michalik-Kucharz et al. (2000) and indicates that there was an invasion of *P. antipodarum* into the water environments of Upper Silesia.

Influence of Physical and Chemical Parameters

The physical and chemical parameters of water play a certain role in the distribution of *P. antipodarum* within the study area. The Kruskal-Wallis one-way ANOVA test revealed statistically significant differences in conductivity, alkalinity, chlorides, total hardness, iron or biogenic elements among reservoirs with non-flowing and flowing water and the river. It seems that *P. antipodarum* prefers relatively higher values of these parameters. Thus, it inhabits reservoirs with flowing water that provide more chlorides from a mine dewatering system and the river that provides more biogenic elements compared to reservoirs with non-flowing water.

Potamopyrgus antipodarum tolerates a wide range of conductivity values from 41 to 3,593 $\mu\text{S}/\text{cm}$ (Costil et al., 2001; Gérard et al., 2003; Sousa et al., 2007b). In this survey, *P. antipodarum* was recorded in water with a relatively high conductivity (from 710 to 3,240 $\mu\text{S}/\text{cm}$). This result is consistent with Costil et al. (2001), who considered *P. antipodarum* characteristic for water with considerably higher conductivity values. Schreiber et al. (2003) also recorded its occurrence in rivers of high conductivity (up to 7,390 $\mu\text{S}/\text{cm}$). This survey showed that both conductivity and the concentration of nitrates were the parameters most associated (statistically significant) with the distribution of mollusc species, including *P. antipodarum*, in the reservoirs with flowing water. This result is opposite to those of Múrria et al. (2008), who showed negative correlations between the abundance of *P. antipodarum* and conductivity or ammonium concentration in water, as well as that of Brzeziński & Kołodziejczyk (2001), who

obtained a negative correlation between its density and the total phosphorus. The results of this survey are consistent with Gérard & Dusart (2003), who showed that *P. antipodarum* density was highly statistically significantly correlated with the concentration of nitrates.

The influence of total hardness on mollusc distribution has been discussed by many authors. For example, Carlsson (2000) found *P. antipodarum* in very soft and soft waters (72.9–145.7 mg CaCO₃/l). In the British Isles, *P. antipodarum* inhabits both soft (Kerney, 1999) and hard water (Fish & Fish, 1989; Kerney, 1999). According to this survey, *P. antipodarum* occurred in medium hard and significantly hard waters in reservoirs as well in significantly hard or hard waters in the Mleczna River. These results confirmed the survey of Strzelec & Krodkińska (1994), Strzelec & Serafiński (1996) and Strzelec (1999b) that *P. antipodarum* prefers hard or very hard waters.

Densities

The density of *P. antipodarum* out of its native range is differentiated from a few individuals/m² in Lake Erie (Levri et al., 2007); up to 49,260 individuals/m² in Lake Purumbete, Australia (Schreiber et al., 1998); 300,000 individuals/m² in the rivers and estuaries of the western part of the USA (Richards & Shinn, 2004) or in the Greater Yellowstone Ecosystem (Kerans et al., 2005) and more than 700,000 individuals/m² in the Upper Owens River watershed in California (Noda, 2007). Low densities of *P. antipodarum* (up to 86 individuals/m²) were recorded in the Mleczna River but there were relatively higher densities up to 7,800 individuals/m² in the mining subsidence reservoirs. This novel finding is in contrast to Strzelec (1993), who recorded densities of *P. antipodarum* from 33 to 999 individuals/m² in the mining subsidence reservoirs in Upper Silesia. High densities of *P. antipodarum* in streams seem to depend on a high primary productivity, constant water temperature and stable discharge (Richards & Shinn, 2004). For example, in geothermal spring streams (Yellowstone National Park) the densities of 500,000 individuals/m² may be explained by the warm and stable water temperature that has an elevated average temperature of 14.4°C in January, as well a bottom carpeted by filamentous algae and vascular plants (Hall et al., 2003). By contrast, long periods of drought, a highly variable water temperature and discharge regimes can reduce the density of *P. antipodarum* (Múrria

et al., 2008). Thus, relatively low densities and the fluctuations of *P. antipodarum* within the survey area throughout the year may be explained by the harsh winter conditions in Poland with an average snow-cover of 42–90 days and ice covering the surface of mining subsidence reservoirs for a few months, as well the management process during summer or autumn (removing macrophytes and regulating reservoirs' output).

This survey revealed a lack of statistically significant differences in *P. antipodarum* density both at the sampling sites in particular months of the survey and at the sampling sites with different types of substratum. These results are in contrast to Richards (2004), who recorded statistically significant differences in *P. antipodarum* densities and types of substratum.

Shell Height

This survey showed that the highest mean shell height (4.42 mm) and the maximum shell height (6.96 mm) of *P. antipodarum* occurred on submerged leaves of *Typha latifolia*, while the lowest mean shell height (3.31 mm) occurred on submerged leaves of *Glyceria maxima*. According to Brown (1997), gastropods prefer the wider leaf blades of macrophytes compared to narrow leaf blades because they provide more periphyton. *Potamopyrgus antipodarum* consumes periphyton, thus the wider leaf blades of *Typha latifolia* (sampling site 1b) probably provide more food (periphyton) than the narrow blades of *Glyceria maxima* (sampling site 1a) or a muddy-stony (sampling site 1c) as well muddy-sandy bottom (sampling site 3a). Thus, statistically significant differences in the shell height of *P. antipodarum* among the sampling sites may be explained by feeding (types of food). Recording the maximum shell height of 6.96 mm may also be explained by the detailed measurements of shell height throughout the year.

Within a native range, maximum shell height in populations of *P. antipodarum* ranges from 4 to 11.5 mm, whereas out of its native range it is almost half the size of specimens within a native range (Winterbourn, 1970). For example, the maximum shell height of *P. antipodarum* ranged from 4.0 to 6.0 mm in the British Isles (Wallace, 1979; Kerney, 1999). In Upper Silesia, the mean shell height ranged from 3.1 to 5.0 mm (rivers and anthropogenic reservoirs) with a maximum shell height of 5.0 mm (Strzelec & Serafiński, 1996; Strzelec, 1999a) compared to a maximum shell height of 5.8

mm in reservoirs with artificially heated water in central Poland (Berger & Dzieczkowski, 1977). This phenomenon, that is, the differences in the shell height of snails within a native range and out of their native range, may be explained by low temperatures as well the influence of poor food conditions (oligotrophic water, high altitudes versus eutrophic water and lowland water environments) on small shell height. Large shell height is a result of higher temperatures, which may permit an increase in the rate and amount of growth (Winterbourn, 1970). For example, the mean annual air temperature in New Zealand ranges from 10°C to 16°C, whereas in Poland it only ranges from 7°C to 9°C. In addition, the larger shell height is more a result of an increase in the number of whorls than in an increase in the size of whorls (Winterbourn, 1970).

Number of Embryos in a Brood Pouch

In Australia, Schreiber et al. (1998) found a maximum number of embryos per female in a brood pouch of 42: the lowest number of embryos was recorded in autumn and in winter, while the highest number was recorded in spring. The results of this survey showed a similar tendency, but the maximum number of embryos was 59 (April). The maximum number of 59 falls between the maximum values recorded by Strzelec & Serafiński (1996), that is, 56 embryos (river) and 66 (sand-pit reservoir) in Upper Silesia. The highest mean number of embryos per female was recorded in April (23.83 embryos), but this is only half the number obtained by Strzelec & Serafiński (1996). In the USA, the number of embryos in a brood pouch found by Cada (2004) ranged from 1 to 83. This survey showed the mean number of embryos of 11.83 ± 10.23 , almost three times lower than that recorded in the USA (Cada, 2004).

Within a native range of *P. antipodarum*, the maximum number of embryos per female amounts to over 100. The number of embryos in the brood pouch is probably a function of the size of the shells (and therefore the brood pouch) (Winterbourn, 1970). In Poland, relatively low temperatures and low food availability during winter may explain the reduction in the growth of snails and therefore the number of embryos in the brood pouch.

A novel finding of this survey showed that *P. antipodarum* produces embryos throughout the year with the lowest mean embryo number recorded in winter (December).

Interaction with Native Freshwater Mollusca

Strzelec (2005) stated that in the anthropogenic reservoirs of Upper Silesia, *P. antipodarum* with a density above 100 individuals/m² may have influenced a decrease in the number of native snail species. In those reservoirs, the increase in the abundance of *P. antipodarum* influenced a decrease in the abundance of *Radix balthica*, *Planorbis planorbis*, *Acroloxus lacustris*, *Segmentina nitida*, *Bathyomphalus contortus* and *Gyraulus albus*. Piechocki & Kaleta (2001) also claimed that a mass occurrence of *P. antipodarum*, with a density of 30,000 individuals/m², may restrict the number of other mollusc species and their abundance. However, their results concerned natural lakes and require further research. This survey does not suggest that *P. antipodarum* with a maximum density of 7,800 individuals/m² has a negative influence on native mollusc species. This result is opposite to Strzelec (2005) because *P. antipodarum* co-occurred with *Acroloxus lacustris*, *Bithynia tentaculata*, *Radix balthica* or *Gyraulus albus* not only in the mining subsidence reservoirs but also in the Mleczna River. A gradual increase in other mollusc species numbers has been observed in these aquatic environments. This result is consistent with Schreiber et al. (2003), who showed a lack of a significant relationship between the presence of *P. antipodarum* and native freshwater snails, and in contrast to that of Ponder (1988) who obtained a negative relationship between the New Zealand mud snail and native snail species. However, it was shown that *P. antipodarum* significantly limited the growth of native snails, whereas the native snails facilitated the growth of the *P. antipodarum* (Riley et al., 2008).

The results of this survey showed the same pattern of densities as stated by Múrria et al. (2008): higher population densities in summer, no effect or a small effect on native Mollusca and stream structure because of smaller *P. antipodarum* densities compared with the western United States survey, where the New Zealand mud snail has a strong influence on stream function including native Mollusca species or other macroinvertebrates (Hall et al., 2003; Kerans et al., 2005; Hall et al., 2006).

CONCLUSIONS

A long-term survey on the occurrence of *P. antipodarum* both in mining subsidence res-

ervoirs and the river in Upper Silesia, which had not been carried out to date permitted an analysis of its initial dispersal, establishment and integration.

Beginning with the initial dispersal in 1997, *P. antipodarum* occurred only in the reservoirs with flowing water and in the Mleczna River. Currently, *P. antipodarum* has been eudominant in the mollusc communities (stage IVb: localized but dominant).

Potamopyrgus antipodarum has established itself in aquatic environments with a wide range of values of many physical and chemical parameters, including conductivity, chlorides, phosphates or the concentration of nitrates in water. The fluctuation in the occurrence of molluscs including *P. antipodarum* may result from the physical and chemical parameters of the water of the mining subsidence reservoirs, which receive water from a mine dewatering system, the management process, and reclamation of the reservoirs. Based on a redundancy analysis (RDA), the conductivity and the concentration of nitrates were the parameters most associated with the distribution of mollusc species including *P. antipodarum*.

The results of this survey revealed statistically significant differences in the shell height of *P. antipodarum* depending on the type of substratum in each of the months of the survey. The maximum shell height amounted to 6.96 mm and was bigger than the maximum shell height of specimens recorded in Poland to date (5.5–5.8 mm).

In the mining subsidence reservoirs in Czułów, *P. antipodarum* is able to reproduce throughout the year. The maximum number of embryos in a brood pouch per female was 59, which is lower than the maximum number of embryos of specimens which occur both in New Zealand (over 100 embryos) and other aquatic environments in Poland (63–66 embryos).

The results of this survey do not suggest that the integration of *P. antipodarum* has negatively influenced the occurrence of other mollusc species either in the mining subsidence reservoirs or in the Mleczna River, probably due to their lower densities compared with the western United States survey, where *P. antipodarum* has a strong influence on aquatic ecosystems and restricts the occurrence of the native macroinvertebrates. *Potamopyrgus antipodarum* has established itself in the mining subsidence reservoirs and integrated itself into the local molluscan species without any major negative effects (e.g. extirpations) on the communities being invaded. However, the ability to

predict the effect of biotic invasions into aquatic ecosystems is still limited. The survey on the establishment and integration of *P. antipodarum* both in the mining subsidence reservoirs and in the Mleczna River should continue.

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